REVIEW ARTICLE

Impact of non-native tree species in Europe on soil properties and biodiversity: a review

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Abstract

In the context of global change, the integration of non-native tree (NNT) species into European forestry is increasingly being discussed. The ecological consequences of increasing use or spread of NNTs in European forests are highly uncertain, as the scientific evidence is either constraint to results from case studies with limited spatial extent, or concerns global assessments that lack focus on European NNTs. For either case, generalisations on European NNTs are challenging to draw. Here we compile data on the impacts of seven important NNTs (*Acacia dealbata, Ailanthus altissima, Eucalyptus globulus, Prunus serotina, Pseudotsuga menziesii, Quercus rubra, Robinia pseudoacacia*) on physical and chemical soil properties and diversity attributes in Europe, and summarise commonalities and differences. From a total of 103 publications considered, studies on diversity attributes were overall more frequent than studies on soil properties. The effects on soil properties varied greatly among tree species and depended on the respective soil property. Overall, increasing (45%) and decreasing (45%) impacts on soil occurred with similar frequency. In contrast, decreasing impacts on biodiversity were much more frequent (66%) than increasing ones (24%). Species phylogenetically distant from European tree species, such as *Acacia dealbata, Eucalyptus globulus* and *Ailanthus altissima*, showed the strongest decreasing impacts on biodiversity. Our results suggest that forest managers should be cautious in using NNTs, as a majority of NNT stands host fewer species when compared with native tree species or ecosystems, likely reflected in changes in biotic interactions and ecosystem functions. The high variability of impacts suggests that individual NNTs should be assessed separately, but NNTs that lack European relatives should be used with particular caution.

Keywords

biodiversity, biogeography, forest management, pairwise stand comparisons, soil impacts

Introduction

Many non-native tree (NNT) species were introduced to Europe, particularly after the 16th century (Brundu and Richardson 2016). Some of these species have been deliberately favoured across Europe through cultivation, mostly because of the different goods and services they provide to societies (Castro-Díez et al. 2019; Brundu et al. 2020; Pötzelsberger et al. 2020a; Castro-Díez et al. 2021). After their initial introductions, some of the NNTs have spread without further human intervention, profiting from suitable soil and climate, competitive superiority and/or habitat disturbance, eventually becoming naturalised, or even invasive (Dodet and Collet 2012). NNTs in Europe include species that are planted for timber (e.g. *Eucalyptus globulus, Robinia pseudoacacia, Pseudotsuga menziesii, Picea sitchensis*; Brundu and Richardson 2016; Brus et al. 2019; Spiecker et al. 2019; Øyen and Nygaard 2020) or once were used for ornamental purposes and have spread since (e.g. *Ailanthus altissima* and *Acacia dealbata*). Overall, NNTs

cover an area of approximately 8.54 million ha, of which *R. pseudoacacia* (2.44 million ha) and *E. globulus* (1.46 million ha) are the most abundant (Fig. 1), corresponding to about 4% of the forest cover in Europe (Brus et al. 2019). This overall percentage hides considerable disparities among European regions and countries. For example, the most abundant tree species in Portugal (*E. globulus*), Hungary (*R. pseudoacacia*) and the UK (*P. sitchensis*) are non-native, while in most other European countries NNTs have a minor importance compared to native tree species (Hasenauer et al. 2016).

The pros and cons of economically valuable NNTs is a topic of lively debate because of the possible detrimental impacts on the ecosystems that may result from the expansion of these species (Campagnaro et al. 2018; Castro-Díez et al. 2019; Pötzelsberger et al. 2020b; Wagner et al. 2021; Wohlgemuth et al. 2021). In addition, NNTs are increasingly discussed in the frame of global change (Brundu and Richardson 2016) and the consequences of climate change on biological invasions and adequate management practices (e.g. Walther et al. 2009). Because of this concern, a large and diverse body of legislation has been created in many European countries, aiming at regulating the establishment of NNTs (Pötzelsberger et al. 2020b). One of the most important pieces of legislation is Regulation (EU) No 1143/2014, the core of which is a list of invasive alien species of concern to the EU, including some NNTs (e.g. *A. altissima* and *Acacia saligna*). Among other provisions, the regulation refers the obligation of the different EU Member States to have in place effective management measures for invasive alien species of EU concern that are widespread. In addition, guidelines on the management of NNTs have been proposed by several authors, aiming at minimising their possible detrimental impacts (Brundu and Richardson 2016; Sitzia et al. 2016; Campagnaro et al. 2018; Brundu et al. 2020).

Among the ecological impacts commonly attributed to NNTs, those related to soil and biodiversity are feasible to measure, functionally important and therefore particularly attractive for research (Hulme et al. 2013). The impacts of NNTs on soil properties can have long-term ecological consequences given the importance of soil as a basis for ecosystem functioning. Among the impacts on soil properties and processes most frequently attributed to NNTs are those related to changes in nitrogen content (Castro-Díez et al. 2009) and other nutrients (Medina-Villar et al. 2016), decomposition rate of organic matter (Godoy et al. 2010), pH (Cremer and Prietzel 2017) and organic carbon (Jackson et al. 2002; Zerva et al. 2005). Soil changes induced by NNTs may be viewed as either beneficial or detrimental, depending on the perspective. For example, an increase in soil nitrogen originated by a leguminous species may be considered beneficial from a farmer's perspective, but detrimental from a conservationist's perspective. It may be detrimental if it alters ecosystem functions and processes of a site or preventing the survival of species naturally-adapted to nutrient-poor soils such as sand dune species (Huston and Smith 1987). However, it may be beneficial if we consider the improvement of soil fertility, for example when rehabilitating mined areas (Dutta and Agrawal 2003; Vlachodimos et al. 2013; Yuan et al. 2018) or improving the conditions for nitrophilous weed species (Yelenik et al. 2004). As to biodiversity, there is certainly a solid argument for the detrimental impacts of NNTs in situations where they reduce richness and diversity of native taxa, or the abundance of native animal or plant populations. A large body of literature has been produced on the

impacts of European NNT species on biodiversity, ranging from microbes (Krevš and Kučinskienė 2017) to plant communities (Chabrerie et al. 2007), invertebrates (Gossner 2016) or birds (Calviño-Cancela 2013).

A large number of papers on the impacts of NNTs has accumulated steadily during the previous century and more rapidly after the launching of the Millennium Ecosystem Assessment (Hassan et al. 2005). Researchers have been particularly keen in conducting comparisons between ecosystems populated by NNTs and native vegetation (NV; mostly native tree (NT) species or native treeless or open ecosystems (OE)), using similar site and climate conditions, to quantify the impact on specific ecosystem properties. Such studies are highly valuable as they often generate robust results based on sound statistical designs. However, the impact of NNTs can be highly context-dependent (Castro-Díez et al. 2019; Sapsford et al. 2020; Castro-Díez et al. 2021), and may vary, e.g. according to the management history of the studied stands, the soil and climate characteristics of the sites, or to the NV to which it is compared. European-wide or global assessments have so far focused on the impact of NNTs on ecosystem services (Castro-Díez et al. 2019), on the impact of mainly invasive plant species on communities and ecosystems (Pyšek et al. 2012), or on the impact of five major NNTs in Natura 2000 sites in Europe (Campagnaro et al. 2018). Nevertheless, a standardised analysis on the impact of NNTs on soil properties and biodiversity based on the existing literature is lacking.

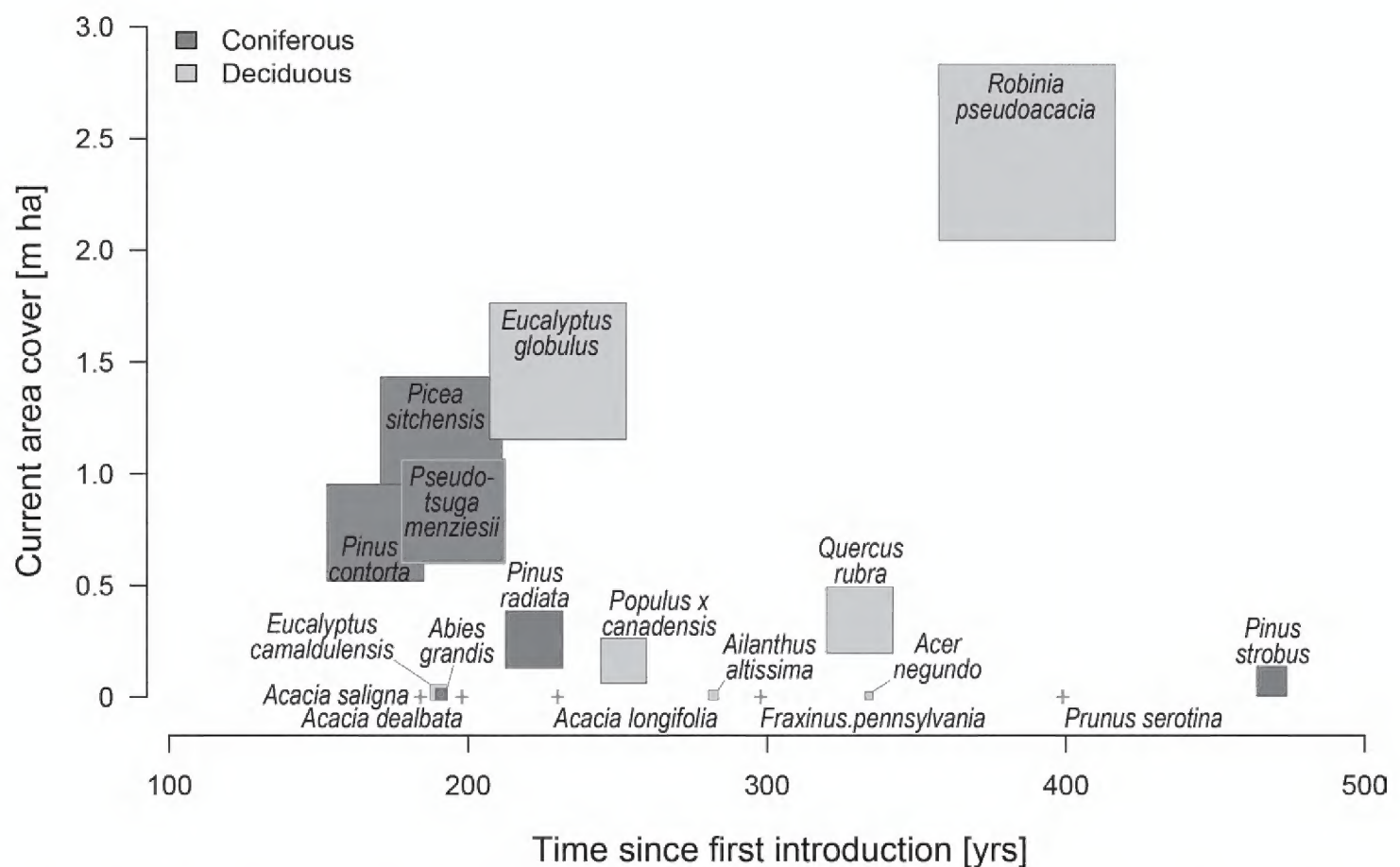**Figure 1.** Current forest area cover of 18 selected NNTs in Europe and year since first introduction (based on Sanz-Elorza et al. 2004; Hasenauer et al. 2016; Badalamenti et al. 2018; Brus et al. 2019). The surface of each square is proportional to the surface covered by each NNT in Europe. The coordinates correspond to the centroid of the square. For NNTs with insufficient information, the symbol '+' is used.

To fill this knowledge gap, here we select seven important NNTs and compile data from a large body of literature on their impacts on soil and biodiversity in Europe, to summarise their commonalities and differences. Specifically, in this study we aim to: (a) assess the relative importance of the different NNTs and their impacts based on published papers, dissertations and reports; (b) assess the impacts of NNTs on soil properties and diversity attributes of different taxa in forests of Europe, based on pairwise comparisons against NV; (c) analyse the commonalities and differences in the impacts of selected NNTs; and (d) discuss the factors that may explain similar or contrasting responses based on available information on NNT traits, biogeography and management.

Materials and methods

NNT selection and workflow

This study was initiated in the frame of the COST Action Non-Native Tree Species for European Forests – Experiences, Risks and Opportunities (FP 1403; 2014–18). From the more than 150 NNTs growing in European forests and forestry trials (Brus et al. 2019), we initially selected the 18 most important ones (Table 1), with their importance assessed according to their forest area cover (if available), and the presence in numerous European countries (Europe defined geographically, but excluding Russia and including Turkey), and/or their rapid spread. We assumed that for the species with these three characteristics, there are likely to be more studies and publications on the impacts. A species is defined as being non-native to Europe if its native range is wholly outside of Europe. Thus, tree species native to Europe but planted outside of their regional distributional range, such as *Pinus nigra*, *Larix decidua* or *Picea abies* were not considered as being non-native even when planted outside of their native range.

The workflow was divided into three phases. In the first phase, we searched the Web of Science (WOS) using the name of the NNT species (e.g. *Prunus serotina*; see Table 1; Fig. 2) as search string. The search covered all papers published until August 2021. Publications retrieved from the search were filtered in order to only retain those featuring pairwise comparisons of NNTs vs. NV regarding effects on physical and chemical soil properties and diversity attributes (abundance, species richness, diversity) of different taxonomic groups studied in European countries. We extended the comparisons with NTs to non-forest ecosystems (OE), as long as they represented a reference for naturalness in the study area. In this phase, four species (*Acacia longifolia*, *A. saligna*, *Eucalyptus camaldulensis* and *Populus × canadensis*) were excluded from further examination due to the low number of studies (n < 20). To increase the number of studies, we extended the search in the second phase to (i) scientific literature with no restriction on language, and (ii) PhD and MSc theses, or other studies published in non-WOS journals or books. Then, the statistical design of pairwise comparisons (NNTs vs. NV) of the selected studies was checked, and the results were examined for analysis of statistical significance, be

it based on tests, figures with error bars, data tables allowing for calculating, e.g. t-tests, or reporting significance. Because of the great variety of indicators used in different studies for assessing differences in soil properties and diversity attributes, the parameters were aggregated, according to Tables 2, 3. Three other species (*Fraxinus pennsylvanica*, *Abies grandis* and *Pinus contorta* var. *latifolia*) were excluded from the analysis because of the low numbers of soil properties or taxa groups concerning these species.

In the third phase, we focused on NNTs having >150 comparisons (cases), where a comparison of NNTs vs. NV regarding one soil property or one species group is one case. As a result, *Acer negundo* (n = 21), *P. sitchensis* (n = 23), *Pinus radiata* (n = 2) and *Pinus strobus* (n = 8) were excluded, leaving seven species: *A. dealbata*, *R. pseudoacacia*, *Quercus rubra*, *E. globulus*, *P. serotina*, *A. altissima* and *P. menziesii*. For the final seven NNTs selected from the 18 focal ones, a total of 103 scientific publications (Suppl. material 1: table S1, fig. 2) with pairwise comparisons regarding soil properties and diversity attributes were included in the analysis. The number of papers found for the NNTs positively correlates with the area cover, with most studies concerning *R. pseudocacia* (n = 32), *P. menziesii* (n = 27) and *E. globulus* (n = 22) (Suppl. material 1: fig. S1). For three species the number of publications was too low (*P. sitchensis*, n = 4; *P. radiata*, n = 1; and *P. strobus*, n = 1), even though these species are among the most widely planted NNTs in Europe.

Table 1. Non-native tree species (NNTs) in Europe considered for literature searches (phase 1), the number of European countries where the species is present (Hasenauer et al. 2016; Brus et al. 2019; gbif.org), total area cover (if indicated, otherwise NA), and selection for final comparisons in regard to a sufficient number of pairwise comparisons. Only NNTs that reached the end of phase 3 had a sufficient number of papers on their impacts.

Family	Species	Origin	Presence in European countries		Considered in study phase
			Countries #	Area [ha]	
Broadleaves					
Fabaceae	*Acacia dealbata*	Australia	5	NA	3
Fabaceae	*Acacia longifolia*	Australia	5	NA	1
Fabaceae	*Acacia saligna*	Australia	10	NA	1
Fabaceae	*Robinia pseudoacacia*	North America	29	2.437.600	3
Fagaceae	*Quercus rubra*	North America	24	345.333	3
Myrtaceae	*Eucalyptus camaldulensis*	Australia	4	20.000	1
Myrtaceae	*Eucalyptus globulus*	Australia	6	1.458.000	3
Oleaceae	*Fraxinus pennsylvanica*	North America	10	NA	2
Rosaceae	*Prunus serotina*	N or C America	14	NA	3
Salicaceaae	*Populus × canadensis*		14	162.274	1
Sapindaceae	*Acer negundo*	N or C America	16	4.724	2
Simaroubaceae	*Ailanthus altissima*	Asia	18	7.142	3
Conifers					
Pinaceae	*Abies grandis*	North America	11	10.459	2
Pinaceae	*Picea sitchensis*	North America	13	1.160.400	2
Pinaceae	*Pinus radiata*	North America	3	257.000	2
Pinaceae	*Pinus contorta* var. *latifolia*	North America	11	736.000	2
Pinaceae	*Pinus strobus*	North America	19	70.382	2
Pinaceae	*Pseudotsuga menziesii*	North America	32	830.707	3

Phase 1

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                    │   Web of Science    │
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                              ◄ ─ ─ ─ ─│ Search: any field="Abies grandis" or "Acacia │
                                       │ dealbata" or … or "Pseudotsuga menziesii"    │
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                    │  24.123     │
                    │ references  │
                    │  18 NNTs    │
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                              │        │ Exclusion: studies that did not conduct      │
                              ◄ ─ ─ ─ ─│ pairwise comparisons in Europe: NNTs vs. NV  │
                              │        │ in stands or single trees nor gradient       │
                              │        │ studies                                      │
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                              │        │ Exclusion: NNTs having a too small number of │
                              ◄ ─ ─ ─ ─│ studies: Acacia longifolia, Acacia saligna,  │
                              │        │ Eucalyptus camaldulensis, Populus x          │
                              │        │ canadensis                                   │
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Phase 2

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│ Addition: publications not  │─ ─ ─ ► │  14 NNTs    │
│ listed in Web of Science    │        └─────────────┘
│ for 14 focal NNTs:          │              │        ┌──────────────────────────────────────────────┐
│ dissertations or reports    │              │        │ Exclusion: publications not meeting          │
│ in local journals cited in  │              ◄ ─ ─ ─ ─│ statistical design, lacking significance     │
│ the WOS papers and from     │              │        │ tests for differences, e.g. standard         │
│ COST collection             │              │        │ deviation/error                              │
└────────────────────────────┘              ▼        └──────────────────────────────────────────────┘
                                     ┌─────────────┐
                                     │  14 NNTs    │
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                                           │        ┌──────────────────────────────────────────────┐
                                           │        │ Exclusion: NNTs with low number of           │
                                           ◄ ─ ─ ─ ─│ traits/taxa groups: Fraxinus pennsylvanica,  │
                                           │        │ Abies grandis, Pinus contorta var. latifolia │
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Phase 3

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                                     ┌─────────────┐
                                     │  11 NNTs    │
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                                           │        │ Exclusion: NNTs with <=150 comparison cases  │
                                           ◄ ─ ─ ─ ─│ → excluding Acer negundo, Picea sitchensis,  │
                                           │        │ Pinus radiata, Pinus strobus                 │
                                           ▼        └──────────────────────────────────────────────┘
                                     ┌─────────────┐
                                     │    103      │
                                     │ references  │
                                     │   7 NNTs    │
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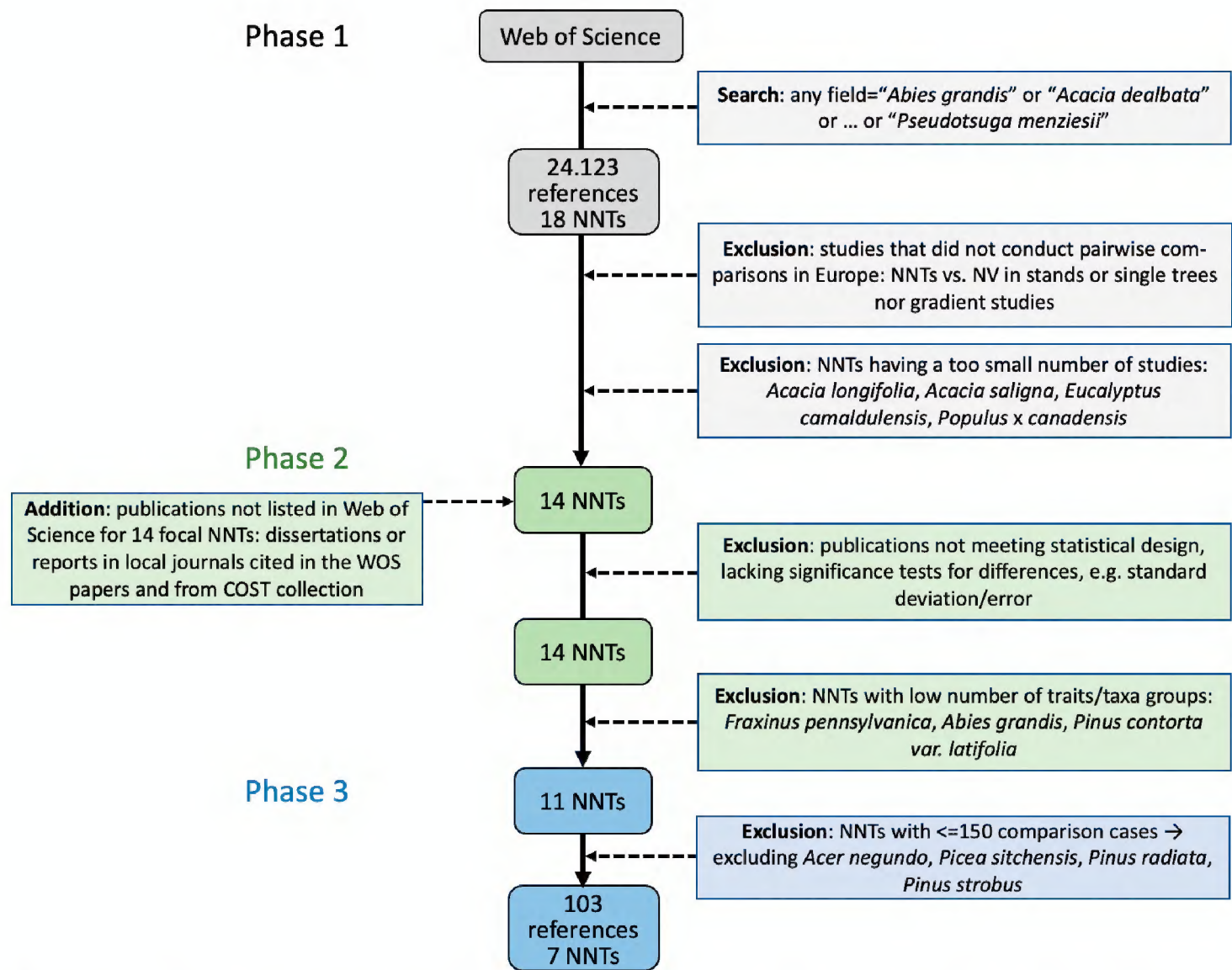
Figure 2. Flowchart of the selection of publications and non-native tree species (NNT). Studies on the effects of NNTs in European forests on soil properties and diversity attributes of different taxonomic groups were considered.

Data analysis

Aggregated soil properties and diversity attributes were counted according to increasing (+1), neutral (0) or decreasing (-1) effects ($p < 0.05$) for the final seven NNTs. The presence of an NNT was considered to have an increasing or decreasing effect if the average values of an attribute reported for NNT stands/individuals were significantly higher or lower when compared with NV stands/individuals. The terms increasing and decreasing relate to the direction of change rather than any judgement about whether the effect on the ecosystem is beneficial/detrimental. While for diversity attributes, increasing effects translate to an increase of abundance- or diversity related attributes, increasing effects with respect to soil properties can be, for some examples, interpreted as having an adverse effect on an ecosystem. For example, an increase in C:N ratio indicates a reduction of N availability, e.g. reduced soil activity.

Due to the great variety of soil properties and diversity attributes used in the studies, comparable traits were aggregated. Cases of increasing, decreasing and neutral effects were counted and used to display differences among NNTs. The numbers then served for transformations to percentages. As these balances reflect all cases found for

Table 2. Most frequently analysed soil properties collected from 103 papers, aggregated and by original description, including number of cases (No); for a complete list of all properties mentioned in the references, see Suppl. material 1: table S1.

Soil properties, aggregated	Soil properties, original	No
N	N, N floor, N foliar, N litter, N mineral, N soil, N stock, N topsoil, N topsoil stock, N total, N total floor, N total topsoil, NH_4+, NH_4+ topsoil, NH_4+, NO_2-, NO_3-, NO_3- topsoil, NO_3-/NH_4+	223
pH	pH floor, pH A, pH B, pH H_2O, pH-H_2O floor, pH H_2O topsoil, pH KCl, pH KCL floor, pH KCL litter, pH KCL topsoil, pH L, pH litter, pH soil, pH topsoil	149
C:N	C:N, C:N A, C:N B, C:N floor, C:N foliar, C:N litter, C:N organic, C:N soil, C:N topsoil	93
Ca	Ca+, Ca+ floor, Ca+ litter, Ca+ soil, Ca+ topsoil, Ca_2+, Ca_2+ exchangeable	70
K	K, K available, K floor, K topsoil, K topsoil available, K total floor, K soil, K total topsoil, K+, K+ floor, K_2O	67
Mg	Mg, Mg floor, Mg soil, Mg total floor, Mg total topsoil, Mg_2+, Mg_2+ floor, MgO	60
P	P, P available, P available topsoil, P exchangeable, P foliar, P total, P total floor, P total topsoil, P total, P_2O_2, P_2O_3, P_2O_4, P_2O_5, P_2O_6, P_2O_7, PO_4	60
CEC	Cation exchange capacity: CEC, CEC floor, CEC litter, CEC topsoil	58

soil properties and diversity attributes, irrespective of whether these cases refer to similar soil properties or closely related taxonomic groups in a specific reference, possible nested cases may lead to biased results. Therefore, averages of cases per aggregated soil property and diversity attribute were also calculated reference-wise and balances were re-calculated accordingly. For example, Buchholz et al. (2015) compared different insect taxonomic groups regarding abundance, species richness and beta-diversity in *R. pseudoacacia* and *Betula pendula* stands in the city of Berlin, Germany. From 17 cases, four were significantly decreasing (-1), and in 13 cases no significant differences were found (0). For this reference, the average effect on insects was calculated as -0.24 (-4/17). Three other references reported all decreasing effects of *R. pseudoacacia* on insects (1× in Reif et al. 2016, 1× in Hejda et al. 2017, and 2× in Kadlec et al. 2018). Averaging for all cases affecting insects, the total effect of *R. pseudoacacia* was calculated as -0.38 (-8/21) for this diversity attribute. In contrast, if the average effect on insects was calculated separately for the four references (-0.24, -1, -1, -1), and then the average total effect was calculated, then the total effect was -0.81 (-3.24/4).

To summarise our results of the effects of the final seven NNTs on soil properties and diversity attributes, we used a Principal Components Analysis (PCA). Effect scores for each NNT are based on total averages. Only the effects with data available for all NNTs were considered in this analysis. All analyses and graphs were developed using the statistical software R version 4.1.3 (R Development Core Team, 2022) and the packages dplyr, ggplot2, rgdal and raster.

Data availability

The data underpinning the analysis reported in this paper are deposited at https://doi.org/10.16904/envidat.350.

Table 3. Most frequent taxa groups (aggregated) from 103 papers, with original taxa groups, diversity attributes, and number of cases (No).

Coarse taxa group	Taxa groups mentioned in the references	Biodiversity measures	No
Vascular plants	Garden natives, geophytes, hemicryptophytes, nemoral plant species, nitrophilous species, rare plant species, road natives, shrubs, small herbs, tall herbs, therophytes, tree regeneration, trees, vascular plants, wood natives	Abundance, biomass, cover, alpha-, beta-, gamma- diversity	720
Microorganisms	Ammonification, ammonification rate, acid phosphotase (AP) activity, bacteria, beta-glucosidase (BG) activity, decomposition, fungi, enzyme activity, glycine aminopeptidase (GAP) activity, geometric mean of enzymatic activities (GMEA), microbes, mineralisation, mineralisation rate, N mineralisation, nitrification rate, soil species	Abundance, activity rates, alpha-diversity	229
Insects	**Blattodea**; **Coleoptera**: *taxonomic:* Carabidae, Staphylinidae, Scolytidae, *functional:* phytophagous, xylophagous, zoophagous, aphidophagous, mycetophagous, copro-/sapro-/necrophagous, omniphagous, saproxylic; **Dermaptera**; **Diptera**: Brachycera (all, Syrphidae), Nematocera; **Hemiptera**: Sternorhyncha – Aphidina, Psyllidae; Auchenorryncha; Heteroptera; **Hymenoptera**: Formicidae, others; **Lepidoptera** (all, moths, Heterocera, larvae); **Neuroptera**; **Psocoptera**; **Raphidioptera**; **Thysanoptera**; *holometabolic larvae*; **other insects** or not further distinguished	Abundance, biomass, alpha-, beta-, gamma- diversity	193
Other arthropods	**Arachnida**: Acari (Acaridida, Actinedida, Gamasina, Oribatidae: Gymnonota, Macropylina, Poronota), Araneae, Opiliones; **Collembola** (Entomobryomorpha, Poduromorpha, Symphypleona); **Myriapoda**: **Chilopoda**, **Diplopoda**; **Isopoda**; **Entognatha**: Protura *Functional arthropod groups*: aerial, micro-/macro, mycetophagous, polyphagous, saprophagous, soil-dwelling	Abundance, biomass, alpha-, beta-diversity	165
Bryophytes	Bryophytes	Abundance, alpha-, beta-diversity	78
Birds	Bird species	Abundance, alpha-diversity	70
Mammals	Bats, carnivores, mammals	Abundance	24
Lichens	Lichens	Abundance, alpha-diversity	17

Results

The majority of the selected studies were conducted in Central Europe and the Western Mediterranean region, while studies on NNTs in the British Isles, North and East Europe (e.g. *P. sitchensis* or *A. negundo*) were excluded because of the low numbers of cases (Fig. 3). Among the NNTs, *P. menziesii* (n = 615), *R. pseudoacacia* (n = 391) and *A. dealbata* (n = 360) accumulated most cases, followed by *P. serotina* (n = 315), *Q. rubra* (n = 230), *E. globulus* (n = 207) and *A. altissima* (n = 158).

In general, the different NNTs were compared with the NV that was dominant in each study region (Suppl. material 1: table S3). For *A. dealbata* and *E. globulus*, Mediterranean pine (e.g. *Pinus pinaster*) and oak species (e.g. *Quercus ilex* and *Q. suber*) but also Mediterranean shrubland types were used for the comparisons. *Ailanthus altissima* was mostly studied in floodplains characterised by the presence of poplar (*Populus* spp.) species. For *P. serotina* and *Q. rubra*, both growing mostly in Central Europe, *Pinus*
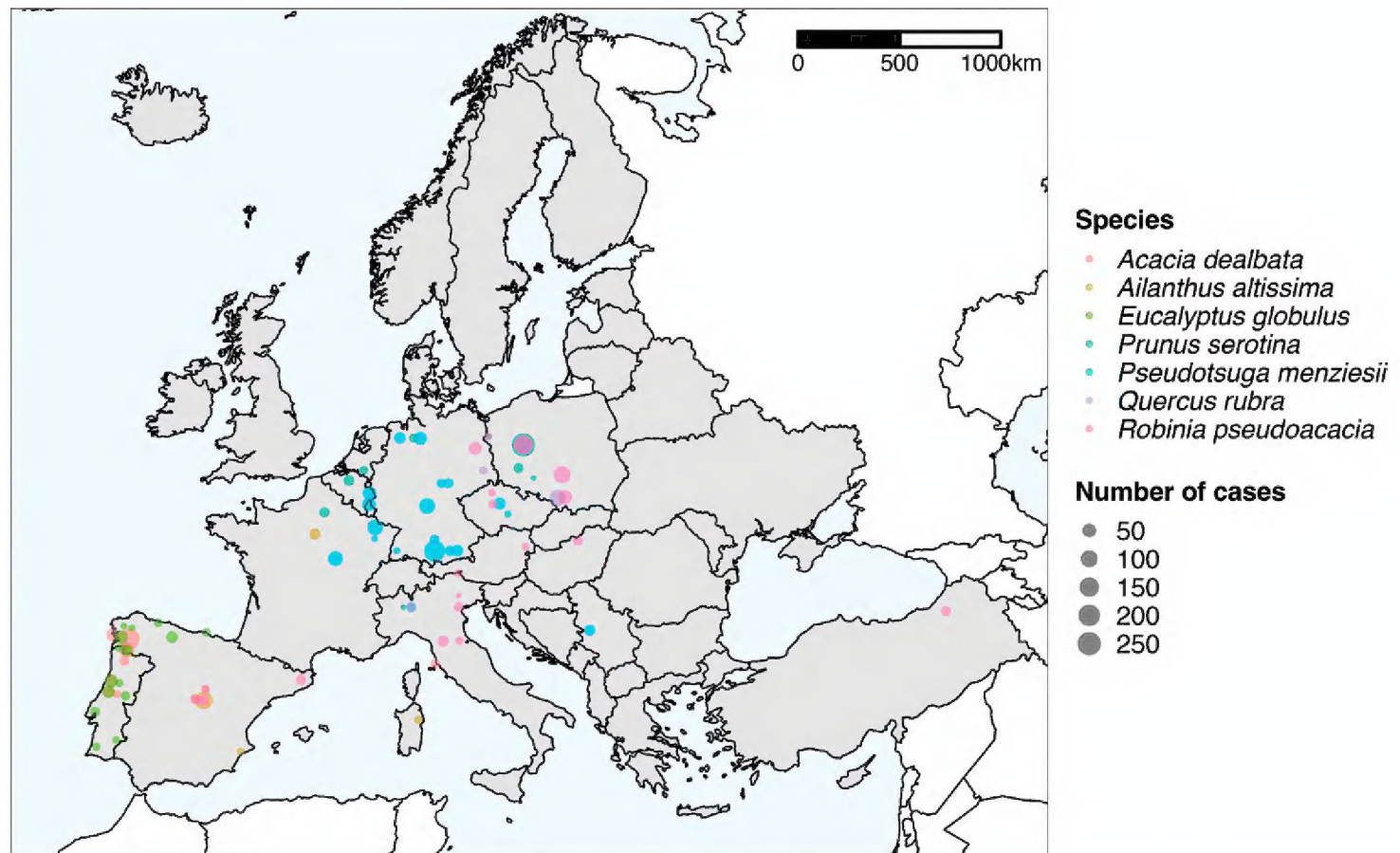
Figure 3. Geographic distribution of studies with pairwise comparisons between tree species non-native to Europe (NNTs; countries considered for this study in grey) and native vegetation (NV), and number of cases for each of the seven NNTs with in total sufficiently high numbers of cases (>150).

sylvestris, oak species (*Quercus* spp.) and *Fagus sylvatica* were mostly the native references. For *P. menziesii*, the native references were mostly *Picea abies* and *F. sylvatica*, and for *R. pseudoacacia* the native references were mostly pine and oak species.

Soil properties

From 780 soil property comparisons collected for the seven NNTs, the aggregated properties N (n = 223), pH (n = 152), and C:N (n = 93) were the most frequently considered properties in the studies (Fig. 4, Suppl. material 1: table S2). Except for cases regarding *P. menziesii*, the other soil properties received little attention, in particular cation exchange capacity (CEC), Mg, K, P and Ca.

The number of cases per species and per soil property was uneven (Fig. 4). Among the NNTs, the most studied was *P. menziesii* with the highest number of overall soil property case studies (n=364), followed by *A. dealbata* (n=135) and *R. pseudoacacia* (n=108). The lowest number of cases was found for *Q. rubra* (n=32). Of all soil property cases considered, 16.9% were decreasing, 61.5% neutral, and 21.5% increasing. Out of 56 possible combinations of eight aggregated soil properties for each of the seven NNTs, the literature review retrieved information on 49 combinations. Of these, impacts were decreasing in 19 cases (39%), neutral in eight (16%) and increasing in 22 (45%).
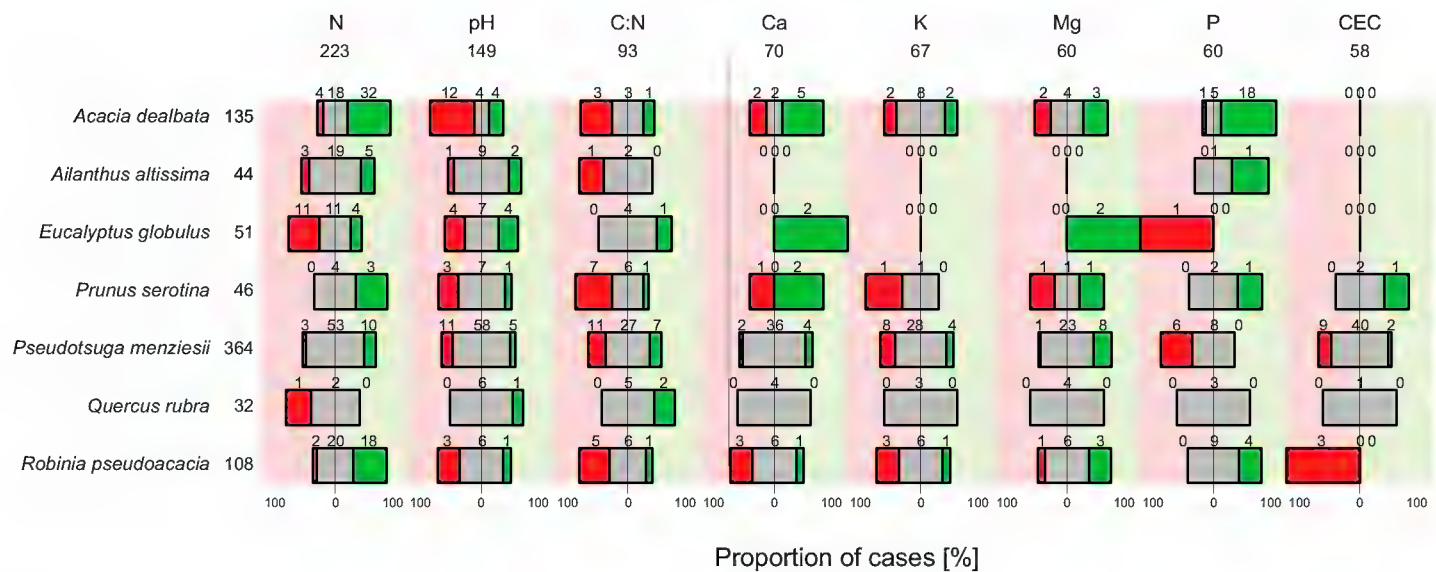
Figure 4. Proportion of cases with significant increasing (green), significant decreasing (red) or neutral (grey; non-significant) effects of the seven tree species non-native to Europe (NNTs) on soil properties (aggregations listed in Table 2) found for each NNT in comparison to stands of native vegetation (NV). Numbers of cases are shown next to the NNTs names, below the soil properties and above the bars. Increasing, decreasing and neutral effects were based on statistical significance (p<0.05).

The following clear trends could be observed: *A. dealbata* increased nitrogen and phosphorus and decreased pH in soils. C:N ratio decreased, e.g. soil activity became higher, in stands of *P. serotina* and *R. pseudoacacia*. In many cases 'no changes' was the most common outcome per species and soil property; in particular, this was observed for *A. altissima* for nitrogen and pH, *P. menziesii* for nitrogen, pH, C:N, calcium, potassium, magnesium and CEC, and *R. pseudoacacia* for pH and, to some extent, also for nitrogen.

Diversity attributes

Of all cases considered, the occurrence of NNTs was recorded as having a decreasing effect in 22.4% of cases, a neutral effect in 65.4% of cases, and an increasing effect in 12.1% of cases.

The number of cases per species and per diversity attribute was more even than for soil properties (Fig. 5). The highest numbers of cases were recorded for *R. pseudoacacia* (n=283), *P. serotina* (n=269) and *P. menziesii* (n=251); whereas the lowest numbers of cases were recorded for *E. globulus* (n=156) and *A. altissima* (n=114). The category vascular plants was the most frequently studied taxonomic group (n=720), while several other groups were rarely studied (birds, bryophytes, mammals, lichens). Most decreasing effects were reported for *E. globulus* and – to a considerable extent – also for *A. altissima*. While in a majority of cases, *P. serotina* presented increasing effect balances, *R. pseudoacacia* had one increasing effect out of seven combinations, *P. menziesii* two increasing effects out of five combinations, and *A. dealbata* two increasing effects out of six combinations. In contrast to the reviewed effects on soil properties,
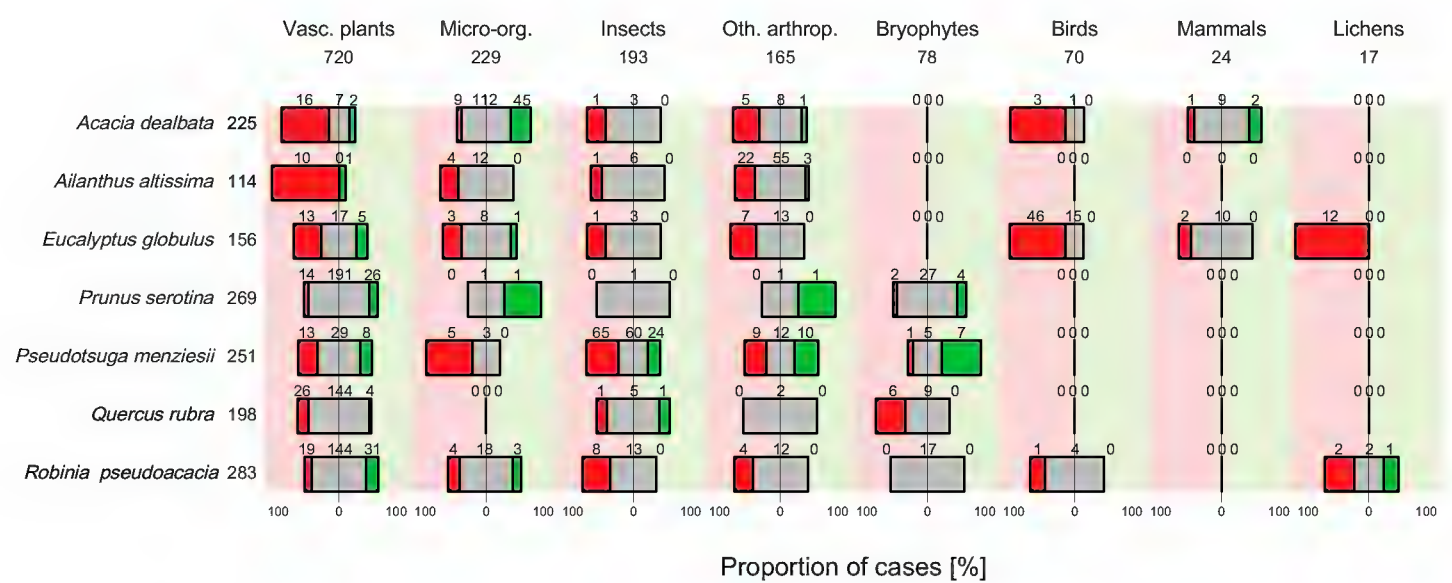
Figure 5. Proportion of cases with increasing (green), decreasing (red) or non-significant (grey) effects of tree species non-native to Europe (NNTs) on diversity attributes (abundance, species richness or diversity) of different taxonomic groups in comparison to native vegetation (NV). Numbers of cases are shown next to the NNTs names, below the diversity attributes and above the bars. Increasing, decreasing and neutral effects were based on statistical significance (p < 0.05).

the consistency of the effects on taxa groups was greater. *Acacia dealbata*, *A. altissima*, *E. globulus* and *Q. rubra* had clearly decreasing effect balances on vascular plant species diversity when compared to native counterparts.

Out of 56 possible combinations, the literature review retrieved information on 38. Out of these balances of NNTs occurrences, 25 (65.8%) had a decreasing effect, 9 (23.7%) an increasing effect, and 4 (10.5%) a neutral effect.

Effects of diversity attributes were finally compared between the two approaches of averaging cases (Fig. 6). Averages using only one value for a taxa group per reference (grey bars) corresponded quite well with averages over all diversity attributes, e.g. taxa groups per NNT (black bars). Only in a few cases, such as vascular plants and bryophytes on *P. serotina* and lichens on *R. pseudoacacia*, did the use of subordinate groups contrast with the averages per reference.

Consistently available soil properties and diversity attributes were used to analyse the different effects of NNTs by Principal Components Analysis (PCA). While cases for all NNTs were available for the soil variables N, P, C:N ratio and pH, three taxa groups (insects, other arthropods and vascular plants) served for comparisons of all NNTs (Suppl. material 1: fig. S2). In the soil biplot, *E. globulus* and *Q. rubra* tended to increase C:N ratio, e.g. decreased soil activity, and increased pH in the case of *Q. rubra*. In the opposite direction, *A. dealbata*, *R. pseudoacacia* and *P. serotina* corresponded to increased N- and P-contents as well as decreased C:N ratio, indicating increased soil activity. Equally, the presence of NNTs (except for *Q. rubra* and *A. altissima*) tended to decrease pH. While *P. menziesii* seemed to slightly decrease soil activity (e.g. increase C:N) and slightly deplete N and P, *A. altissima* corresponded to an increased P content in soils.
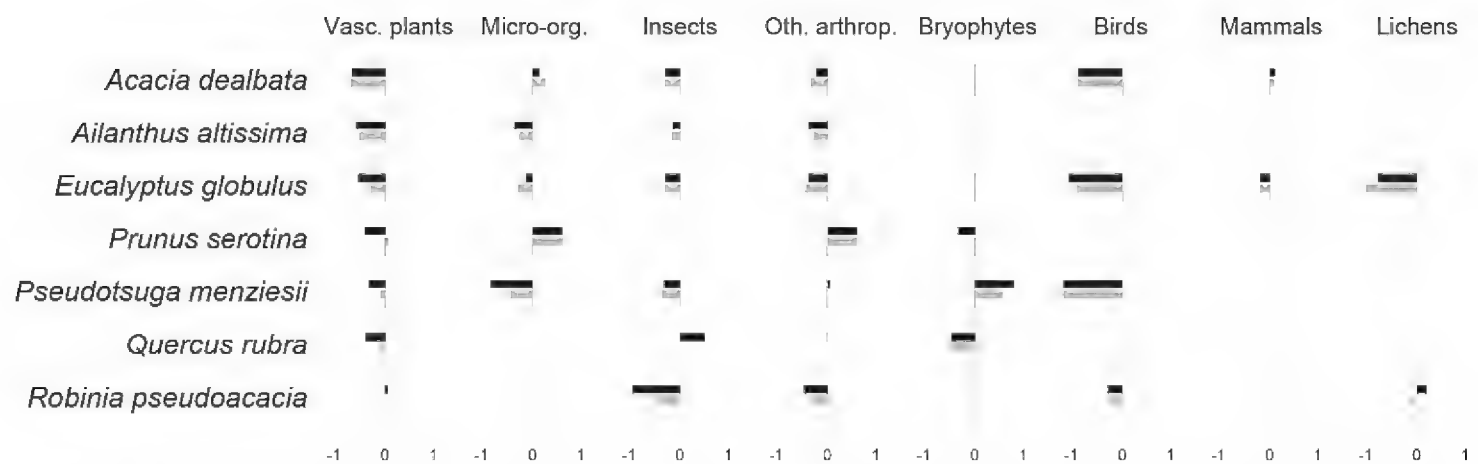
Figure 6. Averaged effects (increasing=1, decreasing= -1, none=0) of tree species non-native to Europe (NNTs) on the most frequently mentioned taxonomic groups. Grey bars indicate averaged effects using all cases (e.g. subordinate groups) found in the references; black bars indicate average values of one value for each reference and taxonomic group (e.g. subordinate groups are averaged per reference).

In contrast to the soil biplot, the biodiversity biplot resulted in complex patterns of taxa groups and NNTs that are mainly driven by the strongest signals of diversity × species interactions and distorting weaker signals (Suppl. material 1: fig. S2). While *A. altissima* and *A. dealbata* clearly decreased vascular plant diversity, most NNTs decreased both insect and arthropod diversity.

Discussion

Most studied NNTs and most studied impacts

The number of comparisons between tree species non-native to Europe (NNTs) and native vegetation (NV) are an indicator of the effort that has been invested by researchers in the study of different impacts of these NNTs on native ecosystems. This effort may give us information on the importance of each combination of species impact for the scientific community (e.g. Pyšek et al. 2020). Our analyses demonstrate that the most abundant studies found on pairwise comparisons between NNTs and NV matched the widespread NNTs *P. menziesii*, *R. pseudoacacia*, *E. globulus* and *Q. rubra*, but also three NNTs (*A. altissima*, *A. dealbata* and *P. serotina*) with comparatively small area cover. In contrast, although the conifers *P. sitchensis*, *P. strobus* and *P. contorta* var. *latifolia* have been quite widely planted, there were too few studies with pairwise comparisons to be considered in our analyses. Most likely, the reason for the disparity between the area occupied and the number of studies (or comparisons) is the invasive status of *A. altissima*, *A. dealbata* and *P. serotina* in several countries, the spread of these species and their impact on native ecosystems during the last decades. Many papers dealing with these species mention their invasiveness in the respective introduction sections, serving as a justification for the study. On the other hand, for the four most studied species (*P. menziesii*, *R. pseudoacacia*, *E. globulus* and *Q. rubra*) there is no

apparent relationship between the area occupied by each species and the number of cases. For example, *P. menziesii*, which is an economically important species in terms of timber production particularly in France and Germany, is by far the most studied species in our database with 615 cases but it occupies only one third of the area of *R. pseudoacacia* (Brus et al. 2019), with 391 cases.

According to our database, the number of comparisons between NNTs and NV was higher for diversity in taxonomic groups than for soil properties. There may be various reasons for this. Researchers can assess a large number of taxa groups in the same study, sometimes using the same plot, as is the case for plant studies. On the other hand, there is a much larger number of taxa to be studied than soil properties. Within the universe of different soil properties, soil nitrogen, pH and C:N, were the most studied, probably because of their ecophysiological relevance for plants and ecosystems, but also because their assessment is relatively easy affordable. As for taxonomic groups, the variation in the abundance of vascular plants was more studied than the variation of all other groups. Methodological reasons, including high costs for sorting and identifying species-rich groups such as insects can explain this imbalance. In contrast, mammals and lichens were the least studied groups of our selection, with the lowest number of cases and the lowest number of NNTs. The difficulties associated with mammal censuses at the scale most NNTs were planted is probably the main reason for the dearth of studies. As for lichens, only a few available studies point to an underrepresentation in such comparisons of NNTs and NV, a phenomenon that may produce bias in the interpretation of NNT impacts (Hulme et al. 2013).

Impacts of NNTs on soil properties

Our results show inconsistent impacts on soil properties. Most studies show no significant effects on soil properties, indicating that in many conditions, other intrinsic local factors, namely parent bedrock, soil type or topography may be more important than the tree species. However, some soil impacts seem to be strongly related to particular tree species. This is the case of nitrogen, which is increased by the two Fabaceae species (*A. dealbata* and *R. pseudoacacia*). This is in line with the findings by Castro-Díez et al. (2019) who found a strong phylogenetic signal in the effect of NNT on soil fertility mostly because of N-fixing species. However, soil fertility comes at the cost of soil acidification as a direct or indirect consequence of nitrogen fixation (Tang et al. 1999).

We would expect fast-growing species, such as *E. globulus*, to produce an increasing effect on nitrogen content due to increased productivity, which could contribute to increase the organic matter by stronger root growth and increased litter input (Evans 2009). However, this was not the case in the studies assessed here. In fact, the short-rotation silviculture (Tomé et al. 2021), and the slow litter decomposition (e.g. Pozo et al. 1998) in *E. globulus* stands, probably leads to lower soil nitrogen content and a concomitant increase in C:N (Castro-Díez et al. 2012; Mallen-Cooper et al. 2022).

Impacts of NNT on biodiversity attributes

The different taxonomic groups were, in a majority of cases negatively impacted by the studied NNTs when compared with the status of local NV. However, there are remarkable exceptions among the eight taxonomic groups examined and among the seven NNTs. With respect to microorganisms, for instance, there were two times more studies showing an increasing rather than a decreasing biodiversity. Most of these studies refer to *A. dealbata*. The results for this NNT may be linked to the results found for soil. The higher nutrient concentration found in most comparisons translates into a higher microbial activity, as found for example by Souza-Alonso et al. (2014). Bryophytes were also increasingly impacted, particularly by *P. menziesii*. Apparently, in this case the moist environment provided by closed and dense canopies of *P. menziesii* stands are likely to cause an increase of bryophytes, while the less shade-tolerant vascular plants declined (Finch and Szumelda 2007). Furthermore, several NNTs had no effect on biodiversity attributes of different taxonomic groups, e.g. regarding vascular plants under *R. pseudoacacia* (Sitzia et al. 2012; Vítková et al. 2017) and *P. serotina* (Chabrerie et al. 2010).

As for vascular plants, the most studied taxonomic group, different reasons may explain the increasing or decreasing biodiversity responses to NNTs, found in our review. *A. dealbata*, *A. altissima* and *E. globulus* were associated with marked detrimental impacts on plant diversity and abundance. In the case of *A. dealbata*, the reasons for the decrease have been related to light competition (Lorenzo et al. 2012), allelopathic effects (Lorenzo and Rodríguez-Echeverría, 2012), and changes in soil nutrients and microbial composition (Rodríguez-Echeverría et al. 2013). Similar reasons were referred to the decreasing plant diversity in stands of *A. altissima*, namely direct competition and allelopathic effects (Motard et al. 2015). The reasons behind the decreasing biodiversity response to *E. globulus*, may be related to intensive management practices. *Eucalyptus globulus* stands are usually coppiced every 10–12 years along three rotations, and the understory is often removed (Tomé et al. 2021). These frequent disturbances may contribute to the decrease of plant diversity (Lomba et al. 2011; Vaz et al. 2019). Other authors, however, point to intrinsic characteristics of *E. globulus* that may be associated to the impact on plant diversity, including the amount of light that reaches the soil, preventing the establishment of shade-tolerant species or the lack of seed-dispersing birds (Calviño-Cancela 2013). Allelopathy, which inhibits germination and root growth of understory plants, has been referred to by many authors (e.g. Souto et al. 2001; Becerra et al. 2018), while a more recent study did not find evidence of allelopathic effects of *E. globulus* on Californian native species (Nelson et al. 2021). This latter work suggests that other mechanisms, such as changes in osmotic potential and water or light acquisition, may better explain the suppression of understory in *E. globulus* plantations. As for *P. menziesii*, the reasons for lowered plant diversity and abundance are normally related with the dense cover of plantations before thinning, strongly shading the ground (Augusto et al. 2002; Finch and Szumelda 2007). In contrast, according to Budde (2006) and Podrázský et al. (2014), species richness and abundance

can be increased in comparison to native stands of *P. sylvestris, P. abies, F. sylvatica* and *Quercus* spp., which obviously strongly depends on management intervention applied to *P. menziesii* stands aimed to support continuous growth and equally increase light transmission. Comparisons of *R. pseudoacacia* stands with NV resulted mostly in non-significant effects, i.e. vascular plant diversity did not differ in the paired stands. There were, however, more cases with increasing than decreasing responses of biodiversity, e.g. Buchholz et al. (2015). Examples with reduced biodiversity highlight the dominance of nitrophilous species in *R. pseudoacacia* stands in contrast to herbaceous vegetation in native forests (Benesperi et al. 2012), or the lack of native plant species adapted to low pH and nitrogen levels in favour of exotic and ubiquituous species in *R. pseudoacacia* plantations (Piwczyński et al. 2016). The fact that an increase in nitrogen was observed in only half of the cases for *R. pseudoacacia* vs. NV may explain why this NNT does not seem to have a general cascade effect on vascular plant diversity.

The higher numbers of increasing vs. decreasing biodiversity responses to *P. serotina* are surprising and reflect the context of the studies considered in the analyses. For *P. serotina*, many increasing cases originate from two studies by Dyderski and Jagodziński (2021a, 2021b), in which several diversity attributes are listed. Most of them refer to *P. serotina* growing in *Pinus sylvestris* stands or plantations and were compared mostly with dense and species-poor *Fagus sylvatica* stands. In contrast, the paper-balanced score in Fig. 6 (in black; only one average value per taxonomic group per paper), results in a distinct decreasing response in vascular plant diversity. This corresponds with many studies that report a reduction in light levels caused by the presence of *P. serotina* (e.g. Starfinger et al. 2003; Chabrerie et al. 2010; Dyderski and Jagodziński 2019).

In summary, it is challenging to disentangle the different factors responsible for a certain impact and to ascertain which factors are more important when it comes to cultivated NNTs (Augusto et al. 2002; Tomé et al. 2021). Similarly to *E. globulus*, plantations of other NNTs are often intensively managed in relatively short rotations to maximise timber production, which results in specific disturbance and light availability regimes across the cultivation cycle (Augusto et al. 2002). These disturbance regimes may include pruning, thinning, understory removal and a clear cut at the end of a rotation. Therefore, cultivation history needs to be considered to better understand the long-term impacts of NNTs on biodiversity (e.g. Carneiro et al. 2008). However, the control for management influence, allowing its separation from the intrinsic species characteristics, is not included in most studies that compared NNTs and NV. The discussion on this topic becomes even more problematic with cultivated NNTs that spread spontaneously and mix with both native and non-native species, such as in the case for *E. globulus* in the Iberian Peninsula (Tomé et al. 2021) and *R. pseudoacacia* in Central Europe (Vítková et al. 2017). More sound conclusions can be drawn from those species that are currently not cultivated and which are considered noxious weeds by national legislations, such as *A. altissima* or *A. dealbata* (Pötzelsberger et al. 2020b). Given their invasive behaviour, there is a strong probability that most stands have been naturally-regenerated and that no management operations have influenced the impacts they cause.

According to our results, the NNTs that cause the strongest impact on biodiversity are those that are phylogenetically distant from European plant species. This is in line with other studies showing the importance of congeneric plant species in the establishment and survival of other living organisms that are part of the ecosystem (Harvey et al. 2012; Spafford et al. 2013). *A. dealbata, E. globulus* and *A. altissima* are associated with the lowest biodiversity in comparison to NV. While, as previously stated, the role of management should be taken into account in the case of *E. globulus*, this role is not a significant factor in *A. dealbata* and *A. altissima*. Therefore, one possible explanation is the lack of eco-evolutionary history with local native species, making it more difficult to establish ecological interactions, such as pollination, herbivory, seed dispersal and entire food webs, in particular when the planted area is small and thus interactions with NV are rare. Nonetheless, there are cases of strong ecological integration of NNTs, such as the case reported for the pollination of *E. globulus* in Galicia, Spain (Calviño-Cancela and Neumann 2015). However, this might occur at the expense of reproductive success and maintenance of native plant populations (Arceo-Gómez and Ashman 2016). The development of these NNT-based novel ecosystems should therefore be taken into consideration when assessing and analysing the impact of NNTs on native species (Hobbs et al. 2006). Besides intrinsic factors of NNTs related to the phylogenetic relatedness (e.g. secondary plant compounds) also structural properties (bark, canopy architecture) as well as co-introductions of associated species can be important in some cases as shown for *P. menziesii* (Gossner et al. 2005; Gossner and Ammer 2006; Gossner 2016).

Conclusions

Our review provides an overview of current knowledge of the effects of NNTs on selected soil properties and diversity attributes and thus a general basis for the discussion on planting and favouring of NNTs in Europe in the face of global change. It shows that despite its relevance, information on the ecological impacts of NNTs is still limited for most species. Our results for seven NNTs with sufficient data suggest that overall impacts on soil properties are low, and in some cases NNTs may even increase soil fertility. However, nutrient enrichment that facilitates the spreading of ruderal or expansive species needs to be carefully assessed, especially in naturally nutrient-poor environments that are particularly important for biodiversity conservation. Significant negative impacts on biodiversity–in particular on vascular plants, insects, and other arthropods–are observed more frequently and suggest a cautious use of NNTs, especially for species that have no close relatives in Europe. In addition to these general trends, our results suggest a strong context-dependency of impacts, especially with respect to focal taxa mainly occurring in different regions and structural properties of the managed stands.

Acknowledgements

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Supplementary material I

Supplementary information

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Data type: tables and figuees (docx. file)

Explanation note: table S1: references and number of comparisons per NNT used from these references: Ps.me=*Pseudotsuga menziesii*, Ro.ps=*Robinia pseudoacacia*, Ac.de=*Acacia dealbata*, Pr.se=*Prunus serotina*, Eu.gl=*Eucalyptus globulus*, Qu.ru=*Quercus rubra*, Ai.al=*Ailanthus altissima*; table S2: all collected soil traits from 103 papers, aggregated and by original description, including number of cases (No), alphabetically ordered; table S3: non-native tree species (NNTs) and percentage of native trees (NT) or open ecosystems (OS) to which the cases compare; figure S1: area cover of eleven non-native tree species (NNTs; phase 3, see Fig. 2; + indicates that the species are present on a relatively small area, the threshold being set at 500 ha for this analysis) vs. number of papers with pairwise comparisons meeting standards; figure S2: biplots of Principal Components Analysis (PCA) using the mean effect of NNTs on four soil properties (left) and three taxa groups (right). Only those variables with a complete set of values for all NNTs were considered for building the PCA.

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